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The Effect of Longitudinal Compression upon the Production of Mechanical Tissue in Stems

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THE EFFECT OF LONGITUDINAL COMPRESSION UPON THE PRODUCTION OF MECHANICAL TISSUE IN STEMS

L. H. PENNINGTON

(WITH TWO FIGURES)

Introduction

For more than a century observations and experiments have been made to determine what factors cause or influence the production of mechanical tissue in plants. Previous to PFEFFER's time, the causes were supposed to be of a mechanical nature. These explanations have been shown to be inadequate.¹ PFEFFER (26, 27) showed that tension, pressure, or even contact may act as a stimulus to cause the production of more mechanical tissue. NEWCOMBE (21) suggested that plants must respond to stress in a self-regulatory manner by producing mechanical tissue where it is most needed. He also indicated the complex notion in regard to stress, and suggested that it should be subdivided. At present we use the terms tension or traction, and pressure or compression, to indicate two opposite kinds of stress

To determine the effect of each kind of stress, much careful experimentation is necessary. HEGLER (12), BALL (1), HIBBARD (14), and BORDNER (2) have investigated the influence of tension upon growing cells, with regard to its mechanical as well as to its stimulatory effects. Although these investigators did not agree in all points, their results show that tension alone cannot cause a very marked increase in mechanical strength. VÖCHTING (34), HIBBARD (14), and BÜCHER (4) have contributed a little concerning the effects of longitudinal compression.

VÖCHTING reported that he fastened weights upon the tops of sunflower stems, some of which had been decapitated, and upon Savoy cabbages, all of which had been decapitated. After leaving the plants thus weighted for several months, he was able to discover

¹ For historical account see URSPRUNG, Biol. Centralbl. 1906.

no increase of mechanical tissue in the sunflower stems, and but a slight increase in the cabbage stems, an increase not at all proportional to the weights used.

HIBBARD suspended weights upon the stems of the sunflower, periwinkle, fuchsia, and coleus, and found in all except coleus a slight response to compression by self-regulatory increase in mechanical tissue. He did not believe, however, that the evidence could be regarded as conclusive.

BÜCHER inclosed both the upper and the lower portions of stems of the castor oil plant in plaster casts, and then fastened these casts so that the stems as they elongated were subjected to a longitudinal compression. All but two of his plants became bent; the two which remained straight were weaker in mechanical tissue than normal plants.

From the few data which have been recorded, it is very plain that we do not have sufficient evidence to show whether or not compression or increased weight may act as a stimulus to cause the production of a greater amount of mechanical tissue in plant stems. General conclusions have been drawn from mere observations of phenomena, which may be due to any one of several influences or to the combination of two or more influences. The few experimental data have led to indefinite or contradictory conclusions. This investigation was undertaken to secure exact experimental data upon the effect of weight tending to produce a longitudinal compression in vertical stems.

Materials and methods

PLANTS USED

From the nature of the experiments, it was necessary to use plants with single upright stems. Both woody and herbaceous plants were used. The woody plants were both one-year-old shoots and seedlings of the common locust (*Robinia Pseudo-Acacia*), both young and one-year-old shoots of sumach (*Rhus glabra*), one-year-old shoots of the poplar (*Populus tremuloides*), and the castor oil plant (*Ricinus communis*). The herbaceous plants were the sunflower (*Helianthus annuus*), the broad or Windsor bean (*Vicia Faba*), and the common bean (*Phaseolus*

vulgaris). The experiments upon woody plants were conducted in the garden during the spring and summer; those upon herbaceous plants were conducted in the greenhouse during the winter and in the garden during the summer.

METHODS OF EXPERIMENTATION

After many preliminary trials, the methods given below were found to be most suitable. For methods other than these, descriptions are given in the account of the different experiments in which they were used. In general, a large series of plants of the same size and age and growing under the same external conditions was used for each experiment. The plants were numbered consecutively. The height and two diameters of each plant were measured, one diameter of the part to be under compression and the other of the part above the compressed region. In case a stem was not cylindrical, the average of the greatest and the least diameter was taken as the diameter of the stem at that place. Strong cords were then looped about each stem at a suitable distance above the ground to serve as an attachment for the weights. The stems were protected from mechanical injury by the cords by first wrapping pieces of soft cloth, commonly known as table matting, around each stem. Each stem was then firmly fastened in a vertical position by tying it to stakes, not in contact with the plant, so that it could not bend or sway, and yet could be restrained in no way except by the downward pull of the weights. Weights were then suspended upon half of the plants, while the other half were left to serve as controls. All plants in a series thus treated were under exactly the same conditions, except that the lower part of each experimental plant was subjected to a compression caused by the downward pull of the weights. If the plants were practically equal in size, alternate stems were weighted; but if they happened to be somewhat unequal, care was taken to see that the average size of the experimental plants was equal to the average size of the control plants. For every large experimental plant, an equally large control plant was chosen, and for every small experimental plant, an equally small control plant was chosen.

More weights were added from time to time according to the

condition of the several experiments. In some experiments the weights were light, scarcely exceeding the weight of the plants; in other experiments they were equal to many times the weight of the plants themselves. Great care was taken to see that the stems were not bent by the weights.

MECHANICAL TESTS

At the conclusion of each experiment, all the plants were measured in the same manner as at the beginning, and the stems taken

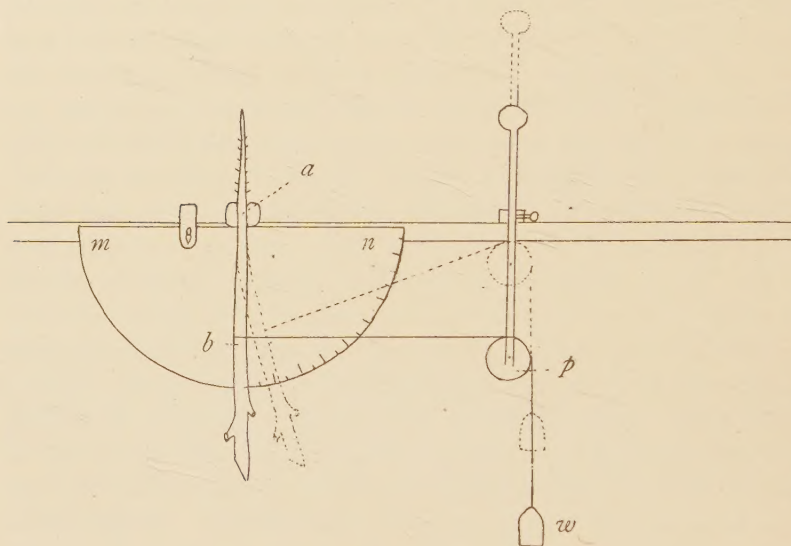


FIG. 1

to the laboratory for mechanical tests and anatomical study. The compressed part of each experimental plant, as well as the corresponding part of each control plant, was tested for rigidity, as shown by its resistance to bending, and for resistance to crushing.

The resistance to bending was determined by a simple piece of apparatus, which is represented by the diagram (fig. 1). The basal end of the stem to be tested was clamped securely at *a*; the cord was looped over the stem at *b*, always at a fixed distance from *a*; the weight *w* was then slowly released and the amount

of bending read in degrees upon the arc of the protractor *mn*. The testing weight for each series of plants was selected so that the plants would not be broken or too strongly bent. The pulley *p* could be adjusted as indicated by dotted lines, in order that the weight should at all times act in the direction perpendicular to the stem. This method was found to show very slight differences in the rigidity of stems.

The resistance to crushing was determined by the apparatus shown in fig. 2. A piece of the stem 10–15 mm. in length was placed with one end against the fixed block *f*, and the movable block *m* brought against the opposite end. The movable block was attached to the strong spring balance *s*, which in turn was attached

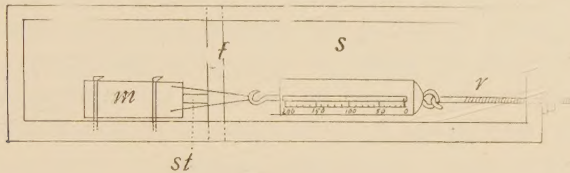


FIG. 2

to the threaded rod *r*. When the tail nut *b* was turned upon the rod *r*, the movable block *m* was drawn toward the fixed block *f*, thus subjecting the stem *st* to pressure. The amount of pressure could be read at once upon the scale of the balance. The resistance to crushing could be determined very sharply, for when the critical point was reached, the stem always gave way suddenly.

After testing a piece for resistance to crushing, the part of the stem next to that which was crushed was put into alcohol to be preserved for a study of the internal structure and microscopic measurements of the mechanical tissues.

ANATOMICAL STUDY

The anatomical studies and measurements were made from cross-sections, which were suitably prepared and stained so as to differentiate more clearly the various tissues, principally the xylem and hard bast. Chemical reactions (aniline sulfate with sulfuric acid, and phloroglucin with hydrochloric acid) as well as stains (acid fuchsin, aniline safranin, and methyl blue) were used.

The method which gave the best results and which was generally used was as follows: Cross-sections of uniform thickness were placed in watch glasses with a little 50 per cent alcohol and two or three drops of alcoholic safranin. In the course of three or four days, all the lignified cell walls were stained a bright red, while other tissues remained nearly colorless. The sections were then either washed in water and mounted in glycerin, or washed in 96 per cent alcohol, cleared in clove oil, and mounted in balsam.

Since xylem forms by far the greatest part of the strengthening, or mechanical, tissue, more measurements were made of this than of the other tissues. For this purpose, exact camera drawings of the lignified parts were made and the area of these drawings determined by means of a polar planimeter. Thickness of wall was determined by taking the average of several measurements, which were made by means of an eyepiece micrometer. Relative size of cells was determined by counting the number in a certain field in the microscope or by micrometer measurements.

In order to avoid the danger of a personal error in making the mechanical tests and microscopic measurements, the stems were numbered indiscriminately by a second person, so that the writer did not know which were experimental and which were control plants until after all tests and measurements were made and the results copied.

Experimental

COMMON LOCUST (ONE-YEAR-OLD PLANTS)

In April, before the growth had begun, 14 one-year-old plants were selected from a large number of sprouts. These plants were measured, tied securely to stakes, and weights suspended upon one-half of them. The cords about the stems were shifted from time to time to avoid constricting the stems as they increased in size. More weight was placed upon the experimental plants, from time to time, as long as they continued to grow. In October, when the experiment was concluded, some of the larger stems were supporting a weight of 20 kilos.

The results for this series of plants were not satisfactory in all respects. Several of the stems were broken or otherwise injured

during the summer. The growth was very unequal in different stems. Some of them increased in size three or four times as much as others, which grew under apparently the same conditions. This is not an uncommon occurrence, however, among shoots which spring from old roots.

Careful comparisons did not show any greater increase in growth or thickness of stem in the experimental plants than in control plants. On the other hand, some of the experimental stems had smaller diameters in the compressed portion than control stems. This diameter in three stems was less than the diameter of the same stem above the compressed part. Although this difference is normally not infrequently noticed in this species, it was rather more striking than usual in these plants. Cross-sections were prepared from experimental stems, control stems, and stems which had not even been tied to stakes. No differences, however, could be seen between any of them.

LOCUST SEEDLINGS

In order to obtain woody stems of more nearly uniform size, seedlings of locust were grown in the greenhouse and transplanted into the garden as soon as the weather became favorable in the spring. Of about 100 which were transplanted, only 30 were considered suitable for experimentation. These were prepared in the usual way and kept under experimental conditions until growth had ceased, about October 15. In the greenhouse, some of the seedlings grew to a height of 15-20 cm.; their stems, however, were very weak. When they were transplanted, they were bent nearly if not quite to the ground by every little breeze, which could scarcely bend locust sprouts which had come up in the garden. In two or three weeks' time, however, these slender seedlings, although they had grown but little in height, had become strong enough to withstand ordinary winds. Some of these slender seedlings were tied to stakes to prevent their being whipped about by the wind. Two or three weeks later, when the stakes were taken away, the plants were still unable to support themselves against a light wind.

This series was kept under the best conditions for growth. The plants were watered frequently during the dry season and protected

from all injury. The final measurements show that the plants grew well. The experimental plants increased 152 per cent in height, 131 per cent in the diameter of the weighted portion, and 122.5 per cent in the diameter a short distance above the weighted part; the control plants, in the same positions and dimensions, 142 per cent, 135 per cent, and 133.7 per cent respectively. The relative amounts of xylem for the experimental and the control plants were 95.17 and 100 respectively. Careful measurements of cell walls showed no difference between the experimental and the control plants.

SUMACH (ONE-YEAR-OLD PLANTS)

From a very large number of thrifty sumach sprouts 24 one-year-old plants were selected for experimentation. In April these plants were tied to stakes, and weights were placed upon the experimental plants in the usual manner. Conditions were fairly good during the growing season. The plants were kept under experimental conditions until October, although nearly all of the growth in size and thickness of stem took place in the spring and early summer. The final measurements and tests showed that the experimental and the control plants were practically equal in size and strength at the end of the season. A comparison of the actual increase in xylem, as determined from the annual rings, showed about 18 per cent less for the experimental than for the control plants. Careful examinations and measurements showed no difference in the size of cells or in the thickness of cell walls.

SUMACH (YOUNG PLANTS)

Sixteen young plants were placed under experimental conditions as soon as they had attained a height of about 35 cm. These plants did not increase greatly in size and thickness of stem. The tests and measurements showed that the strength and amount of xylem were very nearly equal for the experimental and the control plants. The percentage increase was somewhat greater for the experimental plants than for the controls. This difference, however, loses its significance when we observe that the actual increase in height was only 6.93 cm. for the experimental and 5.11 cm. for the control plants, and the increase in diameter only 2.07 mm. and 1.75 mm.

respectively. Careful microscopic examinations and measurements failed to show any differences in cells or cell walls.

POPLAR (ONE-YEAR-OLD PLANTS)

Sixteen plants of the poplar were selected and placed under experimental conditions in April. The plants were measured and carefully tied to stakes. Weights were suspended upon eight of the plants, and as the plants increased in size more weights were added. Although growth practically ceased in early summer, the plants were kept under experimental conditions until October.

The final measurements and tests showed no greater increase in the experimental plants than in the control plants; the increase, in fact, was somewhat less for the former than for the latter. For the experimental plants, the increase in height and diameter of the stem was less than 16 per cent, and for the controls 20 per cent; the relative increase in xylem 77 and 100 respectively; the resistance to bending 81 and 100 respectively. It is difficult to account for these differences. Although the conditions for growth were not good, owing to partial defoliation by insects, they were the same for both experimental and control plants.

CASTOR OIL PLANT (GREENHOUSE PLANTS)

Twenty-four plants of the castor oil plant were selected from a large number which were grown in the greenhouse. Before tying the plants to the stakes, the stems were carefully protected with pieces of table matting. Internodes of bamboo, about 10 cm. in length, were split in two and the halves bound upon opposite sides of each stem, the lower ends extending to within 5 cm. of the ground. Weights were suspended from the upper ends of these pieces of bamboo. In this way room was made for the weights to swing free from the ground, and the longitudinal pressure was confined to the lower 5 cm. of the stems. The plants were kept under experimental conditions for four weeks. The stems were 6 mm. in diameter and 15 cm. high at the beginning of the experiment; they increased about 50 per cent in diameter and 70 per cent in height during the experimental period. At the conclusion of the experiment, the experimental stems were under a pressure of about 1000 grams, equivalent to about 1.33 atmospheres.

The results of the final measurements and tests are shown by percentages. Assuming in reference to each measurement and test that 100 represents the value for the control plants, we have for the experimental plants the following numbers: height at the beginning of the experiment 97.67, at the conclusion 92.33; diameter at the beginning 100.2, at the conclusion 104.5; resistance to bending 120.6; resistance to crushing 104.2. The slightly greater bending and crushing resistances were probably due to the somewhat greater diameter of the experimental plants.

Cross-sections of the stems in this series were prepared and studied with special reference to the hard bast fibers and the collenchyma. The number of hard bast fibers in each stem was ascertained by counting. The average number for the experimental plants was practically equal to the average for the control plants. In each stem the thickness of three collenchyma walls was measured by means of an eyepiece micrometer, and from these measurements the average width of the collenchyma walls determined; there was found to be a difference of only 0.07μ between the two averages; moreover, this excess was on the side of the control plants.

CASTOR OIL PLANT (GARDEN PLANTS)

Eighteen castor oil plants were selected from a large number grown in the garden. These plants were tied to stakes and weighted in the usual manner. They were about 17 cm. in height and 9.5 mm. in diameter at the beginning of the experiment; they increased about 75 per cent in height and 40 per cent in diameter during the experimental period of ten days. At the conclusion of the experiment, the experimental plants were supporting 5-7 kilos each. The usual measurement and test showed no marked differences. Letting 100 represent the value for each control plant average, the following numbers represent the relative values for experimental plant average: height at the beginning of the experiment 101.3, at the conclusion 97.2; diameter at the beginning 101.6, at the conclusion 101.4; resistance to bending 101.8, to crushing 107.5; amount of xylem 109.3.

Another experiment was conducted with 30 selected castor oil

plants, which were divided into three equal sets: experiment plants, control plants, and counterbalanced plants. Each stem of counterbalanced plants was not only tied to prevent bending, but relieved from supporting the weight of the plant itself by tying a cord about the stem, passing it up over a pulley, and attaching a weight to the free end; this weight was kept practically equal to the weight of the plant. These plants were about 20 cm. in height and 9 mm. in diameter at the beginning of the experiment; during the experimental period they increased about 40 per cent in height and 22 per cent in diameter. The growth was less in this experiment than in the former experiment because of more unfavorable weather conditions. The final measurements and tests showed no more marked differences than in other experiments.

SUNFLOWER (GREENHOUSE PLANTS)

From plants of the sunflower which were grown in pots in the greenhouse, 30 of those with straight stems of nearly uniform diameter were selected for experimentation. The stems for this experiment also were bound upon opposite sides with pieces of bamboo to localize the longitudinal compression in the lower portions. More weights were suspended upon the pieces of bamboo from time to time, until at the end of the experimental period of four weeks the experimental plants were supporting a weight of 230 grams each.

The stems were 3.5 mm. in diameter at the beginning and about 5.25 mm. at the conclusion of the experiment. Assuming that 100 represents the value of each measurement and test for the control plants, the following numbers represent the values for corresponding measurements and tests in the experimental plants: height at the beginning of the experiment 99.8, at the conclusion 97.4; diameter at the beginning 95.9, at the conclusion 98.4; resistance to bending 66.7, to crushing 93.5. These numbers show very clearly that there was no greater increase in the experimental than in the control plants. The test for resistance to bending especially showed less strength in the experimental than in the control plants.

Although the mechanical tests would seem to show conclusively

that no increase in mechanical tissue had been caused by weight or compression, cross-sections were prepared and careful examination made to determine the relative amounts of collenchyma, hard bast, and xylem. In none of these tissues could any difference be detected between the experimental and the control plants.

SUNFLOWER (GARDEN PLANTS)

Thirty sunflower plants were selected from a large number of plants and placed under experimental conditions in June. Longitudinal compression was confined to the lower part of the stems by using pieces of bamboo, as in former experiments. Conditions for growth were very favorable. The plants were about 15 cm. in height and 6 mm. in diameter at the beginning of the experiment; during the experimental period of nine days, they increased 100 per cent in height and 70 per cent in diameter. The weights, which were necessarily light at first, were increased daily until the average weight for each experimental plant was 1400 grams (about three atmospheres).

At the conclusion of the experiment the usual measurements and tests, with one exception, were made. Instead of determining the resistance to crushing in this series, the tensile breaking-strength was determined by means of BORDNER'S (2) apparatus. If we assume that 100 represents the value of each measurement and test for the control plants, the following numbers represent the values of corresponding measurements and tests for the experimental plants: height at the beginning of the experiment 105.5, at the conclusion 110.2; diameter at the beginning 94.1, at the conclusion 99.4; resistance to bending 80; tensile breaking-strength 64.2; amount of xylem 80.4. These numbers show that, although the amount of growth in both the experimental and control plants was practically equal, the gain in strength and in mechanical tissue was less in the former than in the latter. The heavy weights evidently retarded the production of mechanical tissue.

A second series of 24 somewhat older sunflower plants was placed under experimental conditions in the usual manner by tying the

plants to stakes and suspending weights upon half of the stems. The plants were 22 cm. in height and 8 mm. in diameter at the beginning of the experiment; they increased about 140 per cent in height and 50 per cent in diameter during the experimental period. The final measurements and tests showed very little difference between the experimental and the control plants.

A third series of 81 selected sunflower plants was divided into three sets and placed under experimental conditions. The first set consisted of 29 experimental plants, the second set of 29 control plants, and the third set of 23 control plants which were relieved from supporting their own weight by cords looped around the stems, passed over pulleys above the plants, and attached to weights, which were kept sufficiently heavy to counterbalance the weight of the stems. The plants in this series were about 38 cm. in height and 10 mm. in diameter, and were kept under experimental conditions ten days. During that time they increased 80 per cent in height and 35 per cent in diameter. Weights were added daily until each experimental plant supported 6-7 kilos.

The usual measurements and tests showed a very great similarity in every respect in all three sets. In no case was there a difference of more than 6.1 per cent between the averages for any two sets. The relative resistance to bending was as follows: experimental plants 106.1, control plants 100, counterbalanced controls 96.2. The relative amount of xylem was: experimental plants 103; control plants 100; counterbalanced controls 98.

WINDSOR BEAN (GREENHOUSE PLANTS)

Several experiments were conducted in the greenhouse with the Windsor bean. Experimental plants tied to stakes and with the longitudinal compression localized in the lower portion, control plants tied to stakes, counterbalanced controls, and plants which grew normally, without additional weight or support, were compared with reference to strength of stem and amount of mechanical tissue. In no case did additional weight or decreased weight seem to have any influence upon the plants. Stems of plants which had been tied to stakes were found to be slightly weaker than stems which had not been tied.

COMMON BEAN (GARDEN PLANTS)

Twenty-four plants of the common bean were selected and placed under experimental conditions. The longitudinal compression was localized in the lower parts of the stems by means of the pieces of bamboo. Measurements and comparisons showed no greater gain in mechanical tissue in the experimental plants than in the control plants:

Discussion

The question of growth and increase of mechanical tissue with special reference to compression may be considered under five heads: (1) heredity and variation; (2) correlation; (3) mechanical effects of compression; (4) stimulatory effects of compression; (5) compression in connection with other stimuli.

HEREDITY AND VARIATION

The production of a certain amount of mechanical tissue in plants is a specific characteristic just as much as is the production of leaves of certain form. Just as leaves of a given species may vary in number and size under the laws of fluctuating variability, so may the amount of mechanical tissue vary. Entirely independent of any known cause, sudden variations may occur in the amount of mechanical tissue formed. The best illustration of this sudden variability is furnished by *Oenothera lutea* (DE VRIES 9), a mutant which does not produce enough mechanical tissue to support its own weight. Another common illustration is furnished by certain lacinate-leaved varieties of the sumach, which have stems too weak to bear their own weight. The difference in the amount of xylem in closely related forms is shown in many grafts. When a scion of one species of elm is grafted upon another species or variety, it soon becomes larger than the branch upon which it was grafted, although there is more mechanical strain upon the branch than upon the scion. The same phenomenon is frequently seen in grafts upon fruit trees.

All of my experiments, especially those in which the weight of the plants was counterbalanced, showed that it is characteristic of each of the species to produce a certain amount of mechanical

tissue. It may be that at some time in the history of a plant it was susceptible to mechanical stresses, and that as a result of these stresses the plant gradually came to develop normally a certain amount of mechanical tissue without regard to the stresses to which it might be subjected. Whether this is the case or not is a mere matter of speculation, so far as this work is concerned, since of course experiments can throw no light upon that phase of the problem. Yet some plants may still be able to respond in a slight degree to such stimuli. It was with this possibility in mind that such comparatively large numbers of plants were used and careful measurements made in order that individual variations might be obliterated in the average of a large number.

It is possible and even altogether probable that the importance of such differences and variations may not have been given the proper amount of attention, or that they may have been overlooked entirely. In this work, however, the possibility of an error from both specific and individual variation has been eliminated by getting the averages of a large number of the same species for each experiment. Further discussion of this phase of the question, therefore, may be omitted. Heredity, however, does have a very important bearing upon the problem in another way.

The ability to produce certain tissues may be hereditary but latent in a plant, and require a certain definite stimulus to make it appear. Many plants do not produce leaves unless they feel the stimulus of light; others, cacti for example, produce leaves only when deprived of light. The experiments of VON DERSCHAU (35) and WORGITZKY (37) show that mere contact may cause the production of a certain amount of mechanical tissue, and contact and strain together are necessary to cause a tendril to produce its normal amount of mechanical tissue. The results of my experiments show that, at least in the plants which were used in this work, no latent hereditary activity is brought forth by compression.

CORRELATION

Under this head may be considered all those observations upon the mechanical tissue in fruit-bearing stems and branches. DENNERT (6), REICHE (29), and PIETERS (28) found in the great num-

ber of instances which they investigated that anatomical changes resulting in greater strength go hand in hand with the development of the fruit. These changes have been attributed both to the strain which is caused by the weight of the developing fruit, and to greater growth activity which is due to the carrying of the greater amount of building material which the fruit demands. KELLER (16) affirmed, however, that the fruit-bearing axis is not strengthened by strain or fruit-bearing in itself, but that the bending of the stem from the orthotropic to the plagiotropic position causes the anatomical changes. It is evident that these observations cannot throw any light upon the stimulatory effect of a tension or a compression acting alone. An experiment by VÖCHTING (34), however, does have a more direct bearing upon the question. He found that by removing the flower buds he could greatly retard the development of the mechanical tissue; the plants were sunflowers and fruiting stems of the Savoy cabbage. He also found that by stress brought about by weighting he could not cause the mechanical elements to reappear (the discussion of this stress is taken up in another place), but when he grafted a scion upon a decapitated stem, the cambium at once began to form the mechanical elements again, although the weight of the scion was equal to only a fraction of the weights which he had placed upon similar plants without result. He sums up the results of his experiments in the following words:

Aus dem mitgetheilten folgt, dass der ontogenetische Gang der Gewebedifferenzierung von inneren, correlativen Verhältnissen beherrscht, dass die Bildung der einzelnen Gewebeformen nicht einfach durch das Bedürfniss bestimmt wird. Die Auslösungs-Theorie genügt hier nicht.

This experiment shows very clearly that correlation may have much more to do with mechanical tissues than mere stress or strain.

Correlation is also seen in many trees in which one-sided growth in the wood is correlated with a greater development of the root system on that side, or with the greater number of branches and the correspondingly greater leaf surface of that side. KNY (17) asserted that one-sided leafing of a tree must be associated with one-sided increase in the growth of the trunk. HARTIG (10) reported that this is the most common cause of eccentric growth in

pine trunks, although there were exceptions to the general rule. WIESNER (36) has attempted to explain eccentric growth in branches by attributing it to unequal size and distribution of the leaves.

In accordance with the observations given above, it was found necessary to keep in mind constantly the correlation between the growth of mechanical tissue and the growth of other parts of the plant. Locust shoots, which at one time were apparently equal and growing under equal conditions, were found to develop at very unequal rates, apparently because of differences in the amount of nutriment stored in the roots from which the separate shoots had sprung.

The differences in herbaceous stems under different conditions are perhaps best illustrated by sunflowers which were grown in the greenhouse and plants of the same kind and age which were grown in the garden. The tall, slender greenhouse plants at the end of four weeks had such poorly developed xylem cylinders that many of the stems were not able to support the weight of the tops, while the garden plants in the same time had become strong and robust, with well-developed xylem cylinders. This is, of course, an extreme case. Many plants, however, which were grown under apparently the same conditions had to be rejected because of abnormalities or differences in growth. By selecting plants which were as nearly uniform as could be obtained, and by keeping all conditions of growth as nearly equal as possible, it was thought that accurate results could be obtained, especially since the possibility of a personal error was also excluded.

MECHANICAL EFFECTS OF COMPRESSION

The textbooks assert that pressure, or compression, retards growth and may completely stop it if the pressure is great enough (PEIRCE 24, JOST 15, PFEFFER 26). It seems no more necessary to make this assertion than to assert that heat, for example, may retard growth or even kill the plant if the temperature be high enough. It is of importance, however, to know whether retardation is proportional to the pressure, and whether changes take place in the cell or in its walls.

The effect upon the plastic growing cell must be the same whether it is compressed or whether it meets resistance to further growth. There can also be no difference in the hydrostatic or the osmotic pressure within the cell, whether the pressure be in one direction or another. In stems a longitudinal pressure causes the cells to exert a greater lateral pressure upon each other, and *vice versa* a lateral pressure must cause them to exert a longitudinal pressure upon each other.

Earlier writers assumed that growth must be inversely proportional to the external pressure exerted upon the growing cells. According to this view, the greatest growth must be in the region of the least pressure. It was upon this assumption that DETLEFSEN (7), SACHS (30), NORDLINGER (23), and KNY (17) sought to explain the eccentric growth of stems and branches. They had then merely to account for a loosening of the bark in some way to cause increased growth. DE VRIES (8) would account for the annual rings by assuming that the bark pressure is greater at some seasons of the year than at other seasons. The experiments, in which he retarded growth and caused the production of smaller cells by putting ligaments around the trunk, showed that great pressure may retard growth, but his relieving pressure by cutting the bark with a knife produced traumatic effects and not true growth. KRABBE'S (18) experiments proved that these theories for unequal growth were erroneous, for he showed that the bark pressure is never great enough to retard growth. This was an indication that growth cannot be directly or indirectly proportional to the pressure. This point was still further emphasized and cleared up by PFEFFER (25). PFEFFER says also (*Plant Physiology* 2:125):

When a root pushes an object in front of it, its rapidity of growth is not perceptibly affected unless the resistance offered is very great.

Although the living protoplasm must control in a large measure the manner in which the cell meets external compression, this subject is discussed under the head of mechanical effects rather than in connection with compression as a stimulus. The manner in which the cell meets external resistance is best told by PFEFFER (*op. cit.*, p. 124):

Under such circumstances [when a plant part is compressed] the tension of the cell walls is gradually replaced by the external pressure, against which the whole osmotic pressure finally acts.

It is thus seen that the plant does not meet a compressing force by growth and cell division, but by osmotic pressure. In reference to growth activity in cells under compression, NOLL'S (22) experiment seems very significant. He showed that in bent roots secondary roots do not arise from the concave side where the cells must be compressed.

HARTIG (11), CIESLAR (5), and SONNTAG (31) attributed the increased thickness of cell walls in heartwood to pressure. Now it does not seem reasonable to think that pressure could cause the walls to become thicker, unless it acts as a stimulus merely to cause greater protoplasmic activity. Since the plant opposes external compression, or resistance to growth, by its osmotic pressure, it would be detrimental to the plant to have the walls lignified before their limits of expansion had been reached. That secondary thickening does not take place until the extension of the cell wall has ceased seems to be the general rule. PFEFFER (*op. cit.*, p. 27) says:

After the stretching growth of the cell has ceased, the cell wall commonly undergoes secondary thickening;

and again (*op. cit.*, p. 32):

An intimate correlation exists between the different forms of growth, and the thickening, cuticularizing, or lignification of the cell wall usually take place when the external growth has ceased.

In regard to the part which the increase in thickness plays in overcoming resistance, we may again quote PFEFFER (*op. cit.*, p. 124):

Even when external growth has ceased, the thickening of the cell walls may still further increase the pressure which the growing tissue is capable of exerting. The observed pressures, however, are *not* greater than could be produced by the osmotic pressure *alone*.

BÜCHER (4) found in his "kamptotrophic" and "geotrophic" stems that thickening of cell walls was always retarded in the parts of the stem which were under compression.

The best experimental evidence of the effect of pressure upon cell walls was given by NEWCOMBE (20). Plant stems were inclosed

within plaster casts; as they increased in diameter, the pressure became greater. It was found that under these conditions the cells remained alive and active, yet the walls remained thin. Even the walls which had already begun to thicken ceased to become thicker as pressure increased.

My experiments in which very young sunflower stems were subjected to heavy weights showed fairly well the retarding effect of a longitudinal compression, for the amount and the strength of the mechanical tissue was found to be less in the experimental than in the control plants.

THE STIMULATORY EFFECTS OF COMPRESSION

Very little is to be found in botanical literature upon longitudinal pressure, or compression, as a stimulus, and still less as to its effect or lack of effect upon mechanical tissues. In nearly every instance in which the stimulatory effect of pressure is mentioned, it is loosely applied or very evidently connected with other causes of stimulation. PFEFFER states (*op. cit.*, p. 124):

Various stimulatory influences are exercised by tension, pressure, and mechanical vibrations or disturbances.

What he says concerning the influence of compression has already been discussed under mechanical effects.

In nearly all researches, compression has been associated with other stimulatory influences. Those observations in which the author attributed the observed effects to pressure, or compression, are discussed under this head.

HARTIG (10) found that trees which were subjected to the action of a west wind produced thicker annual rings upon the east side than upon the west side. His explanation is best given in his own words:

Der Druck des Windes übt einen Reiz auf das Plasma der Cambiumschicht aus, welche in zweckentsprechender Weise durch gesteigertes Wachstum und durch Dickwandigkeit der Organe auf diesen Reiz reagirt.

These observations have not been confirmed by experiment, and URSPRUNG (32) has shown by his observations and experiments that longitudinal compression cannot account for these phenomena.

CIESLAR (5) bent four young spruces at right angles so that the upper parts lay in a horizontal plane, and kept them bound in that position for two years. He found the greatest increase in the thickness of annual rings to be in the concave or compressed side. From this experiment he concluded that pressure causes the greater increase in growth. The objections to this conclusion, however, are obvious. CIESLAR apparently did not consider the tension upon the convex side, nor the one-sided effect of gravity, which must produce a geotropic influence as soon as the tree is bent from the perpendicular position. The same objections may also be made to SONNTAG'S (31) conclusions.

VÖCHTING'S (34) experiments, however, require more consideration. VÖCHTING'S report of his experiments leaves room to question whether his plants were placed under longitudinal compression, tension, or a combination of the two. After finding that sunflower and cabbage plants, which had been decapitated to prevent fruiting, did not produce the normal amount of mechanical tissue, he says:

Zunächst und vor allem fasste man die mechanischen Zellen in's Auge. Nach HEGLER'S bekannten Angaben kann man durch künstliche Belastung nicht nur eine raschere Entwicklung dieser Elemente herbeiführen, sondern ihre Neubildung sogar an Orten bewirken, an denen sie sonst nicht entstehen. Ist diese Angabe, die durch unsere eigenen Erfahrungen nach gewissem Richtung bestätigt wurde, richtig, dann darf man erwarten, dass die veränderten Objecte unseres Versuches, wenn künstlich belastet, die mechanischen Elemente wieder hervorbringen. Von dieser Voraussetzung ausgehend wurden am Blühen verhinderte Pflanzen des Wirsing und der Sonnenblume durch Gewichte belastet, die in geeigneter Weise am Scheitel angebracht waren; bei der zuletzt genannten Pflanze wurden ausserdem noch normal blühende Objecte zum Experimente verwandt. Die Belastung war verschieden gross; die grösste betrug bei der Sonnenblume 20 Kilo, beim Wirsing mehr als 6 Kilo, Gewichte, die das der Blüten- und Fruchtstände, welche, unter gewöhnlichen Verhältnissen von der Pflanze erzeugt werden, um ein Vielfaches übertreffen. Die Belastung dauerte Monate lang.

If we understand by this that the writer had in mind HEGLER'S (13) experiments in which stems were subjected to tension or pull, we should take this "geeignete Weise" to mean that weights were fastened so as to exert a pull upon the stems. This is the interpretation placed upon it by BALL (1), HIBBARD (14), and BORDNER (2).

If, on the other hand, we take the meaning in the general sense, that a plant responds to the demands ("das Bedürfniss") made upon it, we may interpret the phrase to mean that he fastened the weights in such a way as to simulate the tension caused by the fruiting head. BÜCHER (4) interpreted this to mean a longitudinal pressure or compression, as indeed it must if the fruiting heads remained erect. Since, however, the fruiting head of a sunflower droops, it must exert tension upon the part of the stem next to it, and both tension and compression in the bent part, tension upon the upper or convex part and compression upon the under or concave part. It seems from a later statement of VÖCHTING'S that the stems were kept erect. In that case, the "Belastung" must have exerted a compression only. He says in summing up his results:

Wir fanden, dass selbst sehr starke Belastung der *aufrechten* am Blühen verhinderten Objecte nicht genügt, um das normale Holzwachsthum wieder herbeizuführen.

BÜCHER found weaker development of the mechanical tissues and less cambial activity in the two castor oil plants which he subjected to longitudinal compression than in normal plants. The stems were also larger in diameter, owing to the abnormally large thin-walled cells.

HIBBARD (14) used the same general method for subjecting stems to compression that I have employed in this investigation. His experiments were of a preliminary nature, comparatively few plants were used, and there is no record of his making mechanical tests or exact measurements of the mechanical tissue. When so few plants are used and no averages made, errors from individual variation may easily occur. It is not certain that the possibility of personal error was eliminated, although he says that the same conclusions were arrived at by two persons working independently.

In reference to HIBBARD'S experiments as well as to my own, a question may arise as to whether a stimulus is really exerted by such means as were used. This question may be answered in several ways. It is well known that living protoplasm is very sensitive. This sensitiveness is shown by the responses of *Mimosa*

leaves and by tendrils. The researches of BOSE (3) have shown that the protoplasm of other plants and plant parts is equally sensitive, although the plant cannot respond by a perceptible movement. In case growth is retarded, as it was in some of the experiments, the protoplasm must necessarily feel the effect. It has been demonstrated that there are interacting stresses in plants, of which a good example is afforded by twisted tree trunks. Force is required to cause such a twisting. If the weight of the top is the force, twisting must be accompanied by a shortening of the central cylinder or by an elongation of the outer layers. In either case, a longitudinal compression must be exerted upon the outer cells. It is not certain that the inner cylinder may become shorter, but it has been shown that wood cells may increase in length from the center to the circumference of a tree trunk. If this elongation of cells tends to lengthen the outer layers of wood in straight trunks, increased weight upon the trunk must alter the internal equilibrium of stresses, for it not only acts directly upon the outer layer, but it tends to increase the retarding action of the inner cylinder. Moreover, it is not safe to say that the woody cylinder is so rigid that it cannot change, for we know that wood is more or less elastic, and that the limit of elasticity may be exceeded by either great pressure or great tension. If a bar of wood is forcibly bent and kept in that position for some time, a readjustment takes place so that the bar remains bent without the external force. The sensitive protoplasm in a cambium layer, which surrounds closely a cylinder of wood, must feel very slight changes that might occur in the cylinder.

If the weight of the plant can furnish a stimulus for production of increased mechanical tissue, this stimulus must be lacking when the stem is relieved from supporting the weight of the plant. For the same reason an increased weight, equal to two, four, ten, or twenty times the weight of the plant, ought to produce a response by an increase in the strengthening tissue. Assuming that plants do respond to various stresses by becoming stronger, and that they remain weak if relieved of all stress, then the plants used in my experiments were placed under the most favorable conditions to respond to a given stress, for they were relieved of all stress except

the downward pull of the weights. In no case, however, were they found to become stronger mechanically. It must be concluded that a longitudinal compression, acting by itself and acting continuously upon a plant stem, cannot stimulate it to greater activity, nor to an increased strengthening of the tissues that are already present.

COMPRESSION IN RELATION TO OTHER STIMULI

For convenience, we may separate the stimulatory influences into three groups: the so-called internal stimuli, environmental stimuli, and strains or stresses. These internal stimuli may be due indirectly to environmental conditions. Since we know little or nothing about them, it is convenient to refer to this group all those phenomena which we cannot attribute to definite external conditions or stimuli. Environmental stimuli include gravity, light, heat, moisture, etc. Strains or stresses are tension and compression.

In nature the various influences are intimately associated with each other, and often so modify one another that observers and sometimes experimenters have overlooked certain influences and thus given undue weight to others. As an example we may speak of HARTIG'S observations and CIESLAR'S experiments in which pressure only was considered, where evidently gravity, tension, and perhaps other influences may have played an important part.

Others, who were not able to account for observed phenomena by certain external stimuli, explained them by saying that they are due to internal stimuli. As an illustration, a quotation from MASSART (19) will serve very well. In speaking of root swellings and eccentric growth in *Ficus* roots he says:

L'épaississement asymétrique est régi par la gravitation, par la lumière et par des excitants internes, encore indéterminés.

Experimenters who examine more closely into the reactions of plants are forced more and more to the conclusion that the plant acts as a unit in a self-regulatory manner to bring about the greatest good to itself. NEWCOMBE (21) was the first to point out the necessity of considering the self-regulatory power of plants with special reference to their response to stress. URSPRUNG (32, 33) came to practically the same conclusion after a series of observations upon eccentric growth in trunks and branches.

BÜCHER (4) also arrived at this conclusion as a result of trying to bring his results into harmony with BALL'S (1) conclusions.

The application of the self-regulatory theory may seem to serve merely as a term to cover our ignorance. In reality it throws much light upon the whole question of stimulatory reactions, since it shows the great number of possibilities. In order to determine the influence of one factor, all the others must be taken into consideration, and their influence either eliminated or equalized by the use of both experimental and control plants under exact experimental conditions.

Considerable investigation has been carried on with respect to the various environmental stimuli. Further discussion of them, however, is not necessary in this place. In regard to the stimulatory effect of stresses and strains, comparatively few exact data have been obtained.

If we consider BORDNER'S results in regard to tension, it seems that a little more definite conclusion may be drawn from BÜCHER'S, as well as from my own experiments. BÜCHER found that when a stem is bent and then placed upon a klinostat the cell walls on the convex or tension side become thicker, and on the concave or compression side the walls remain thin, while the cells themselves become larger. In stems which were held in a horizontal position so that they could not bend upward under the stimulation of gravity, he observed the same results; the upper or stretched side had normal or slightly smaller cells with thickened walls, while the lower side had large thin-walled cells. Now BORDNER'S results show that, under proper experimental conditions, tension causes a strengthening of stems by producing thicker walls; and it is shown that compression, when not too great, causes large thin-walled cells. It seems reasonable to say that tension and compression may be given as the two direct influences for the results observed by BÜCHER.

It is evident that the tension and compression do not have exactly opposite effects. We have seen that compression causes the cells to become larger and thus give greater surface for the osmotic pressure. Tension, as shown by the experiments of NOLL and HEGLER, tends to accelerate growth and cell division.

The two influences of tension and compression are thus both favorable to increase in the size of the organ subjected to them. Then if we accept the view of HEGLER and BORDNER, that tension may cause the walls to thicken, we have in an alternation of tension and compression all the necessary stimuli for increased size, growth, and strength in the part subjected to those stresses. It does not seem unreasonable to assume that intermittent or alternating compression and tension should have a greater stimulatory effect than a constant stress. It is very possible that under constant stress the internal equilibrium of stresses may come in time to be readjusted so that the external stress would be no longer felt. In experimental work this objection may be removed in part by increasing the stress from time to time. Yet it is easy to see that this could not have so much influence as the complete reversing of the stress from tension to compression and *vice versa*.

Summary

In the foregoing work the four woody stems show no increase in mechanical strength or in the amount or kind of mechanical tissue under the influence of longitudinal compression.

In young herbaceous stems the development of mechanical strength in the tissues is somewhat retarded by a longitudinal compression caused by comparatively heavy weights.

Neither light weights nor heavy weights have any appreciable effect upon the growth and strength of herbaceous stems which have already formed a cylinder of mechanical or woody tissue.

Continuous longitudinal compression causes no marked differences in the size or form of any part of the stem which is subjected to the compression, excepting of course mechanical changes which might be caused by excessive compression.

The investigation for which these results were obtained was carried out under the direction of Professor F. C. NEWCOMBE, to whom I wish to acknowledge my sincere thanks for his kindly interest and timely suggestions.

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